

DIVERSITY, NATURAL HISTORY, AND CONSERVATION
OF VANILLA (ORCHIDACEAE) IN AMAZONIAN WETLANDS
OF MADRE DE DIOS, PERU

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ABSTRACT

Investigations of the diversity and natural history of *Vanilla* are scarce, especially in the Amazon region. Considering that the cured, fragrant fruits of several species are traded in international markets and are an important cash crop for thousands of small-scale farmers in tropical regions, there is a surprising lack of published information concerning *Vanilla* in the botanical literature. This paper presents the results of a study of six *Vanilla* species that occur primarily in wetland ecosystems of Madre de Dios, Peru, in the southern Peruvian Amazon. While extremely rare outside wetlands, the genus is one of the most conspicuous elements of wetland vegetation due to its high visibility and abundance, yet it is virtually unknown even to local residents. Here we describe each species in detail with notes and observations from field studies of their natural history. We also offer a key for their identification. We conclude with a discussion of conservation implications and recommendations for continued investigation of *Vanilla* orchids and their Amazonian wetland habitats.

KEY WORDS: *Vanilla*, Orchidaceae, Peru, Amazon, wetlands, diversity, natural history

RESUMEN

Investigaciones de la diversidad e historia natural de *Vanilla* son escasas, especialmente en la Región Amazónica. Considerando que sus frutos curados y fragantes provenientes de diversas especies son comercializados en mercados internacionales y que son una considerable fuente de ingreso para miles de productores de pequeña escala en las regiones tropicales, resulta sorprendente la ausencia de información publicada acerca de *Vanilla* en la literatura botánica. Este artículo presenta los resultados del estudio realizado en seis especies de *Vanilla* provenientes de los humedales de Madre de Dios, Peru, ubicados al sur de la Amazonia Peruana. Si bien es extraño observarlo fuera de humedales, este género es uno de los elementos más conspicuos en la vegetación inundable debido a su visibilidad y abundancia, y aun así es virtualmente desconocido para los lugareños. En el presente artículo se describe cada especie en detalle con notas y observaciones de estudios de campo y de su historia natural, e inclusive ofrecemos una clave para su identificación. Para finalizar concluimos con una discusión de las implicaciones en su conservación y recomendaciones para realizar investigaciones posteriores en *Vanilla* y de su habitat inundable amazónico.

INTRODUCTION

Vanilla Plum. ex Mill. is a pantropical genus of the Orchidaceae comprising more than 100 species of epiphytic and terrestrial lianas. It is noteworthy among the genera of the Orchidaceae tribe Vanilleae as the most species-rich, widespread genus (Stern & Judd 1999). Based on recent molecular studies the vanilloid orchids are recognized as an ancient lineage that deserves to be treated as a subfamily of the Orchidaceae (Chase et al. 2003; Cameron 1999). Such attributes highlight *Vanilla* as key to understanding the orchid family, arguably the most species-rich group of plants on the planet, calling for further studies of the diversity and natural history of this genus.

Taxonomic investigations are scarce or incomplete and the genus is plagued by lack of collections, misidentifications of existing collections, poor understanding of species concepts, and a conflicting synonymy

(Chevailier 1946; Correll 1946). Two major revisions of the genus by Rolfe (1896) and Porterès (1954) are largely out of date. Recent molecular studies (Bouetard et al. 2010; Soto-Arenas & Dressler 2010) have greatly improved our understanding of the phylogenetic relationships between species; however, these are still tentative and incomplete. Soto-Arenas and Cribb (2010) have recently revised the infrageneric classification of the genus, lamenting that our knowledge of *Vanilla* is far from adequate to produce a good, modern revision.

Exacerbating taxonomic problems, there is a deficit of natural history studies and the observations that come from them, such that even basic information concerning dispersal mechanisms and pollinator relationships remains enigmatic. Several characteristics of the group make detailed investigation, documentation, and collection difficult. First, *Vanilla* species often occur in low-density populations that are hyper-dispersed in local areas of their limited geographic ranges (Soto-Arenas et al. 2003). This has contributed to the lack of herbarium collections and basic natural history data. Second, plants are usually encountered without flowers as many species require pendant growth in bright light to initiate budding. Third, the succulent nature of the plants renders them very slow to dry and botanical collectors often avoid them as logistically problematic. Finally, *Vanilla* species often have delicate, ephemeral flowers that do not preserve well on herbarium specimens.

From an economic perspective, cured *Vanilla* fruit provide the world's major source of natural vanilla fragrance and flavoring. In 1995, fruits from *Vanilla planifolia* ranked as the leading U.S. spice import on par with black pepper (Buzzanell & Gray 1995). World production estimates in 2001 of approximately 2300 metric tons (Loeillet 2003) are generally restricted to developing tropical countries with a cheap labor force (Koekoek 2005; Anonymous 2003). The crop is important to thousands of small-scale farmers worldwide, with highest production coming from Madagascar and Mexico (Hermans and Hermans 1995). However, the narrow genetic base of commercial *Vanilla planifolia*, due to strictly vegetative propagation, and its growing susceptibility to viral and fungal pathogens suggest that the industry has not fully explored the genetic resources harbored by potentially disease-resistant wild species (Besse et al. 2004; Grisoni et al. 2004; Bory et al. 2008).

Modern studies of the diversity and natural history of *Vanilla* are needed in the Amazon. Amazonian species of *Vanilla* have been poorly collected and are little known in comparison with Central American species (Soto-Arenas, pers. comm. 2007). During ongoing studies of the diversity, natural history, and conservation of wetland plants and ecosystems in Madre de Dios, Peru, by the Botanical Research Institute of Texas (BRIT), six *Vanilla* species have been encountered. The goal of this paper is to provide an updated report of the diversity of *Vanilla* species in Madre de Dios wetlands, with comparisons to the historical collection record and knowledge of the genus in the Amazon. Most species are newly recorded for Peru. Morphological descriptions and a key are provided along with notes and observations to document current knowledge of the distribution, habitat, and natural history of each species. We follow this with a discussion of important conservation implications.

MATERIALS AND METHODS

Study Site

All studies were carried out along the Madre de Dios River watershed in the Department of Madre de Dios, located in southeastern Peru and corresponding to the headwaters of the southwestern Amazon (Fig. 1). The region is widely recognized as a hotspot of biological and cultural diversity that is partially protected by a series of large conservation areas, including Manu National Park, Bahuaja-Sonene National Park, the Tambopata Reserved Zone, Los Amigos Conservation Area and the Amarakaeri Indigenous Reserve. The study region includes flat lowland habitat ranging in elevation from 300 to 350 m classified as humid tropical forest. Wetlands with hydromorphic soils, generally dominated by palms, are a patchy, but ubiquitous aspect of the landscape in topographical depressions and in the vicinity of seepages (Kahn 1987; Kahn & Mejia 1990). Along current river floodplains wetlands are a prominent habitat, becoming quite extensive and ranging in size from 10 to 3000 ha.

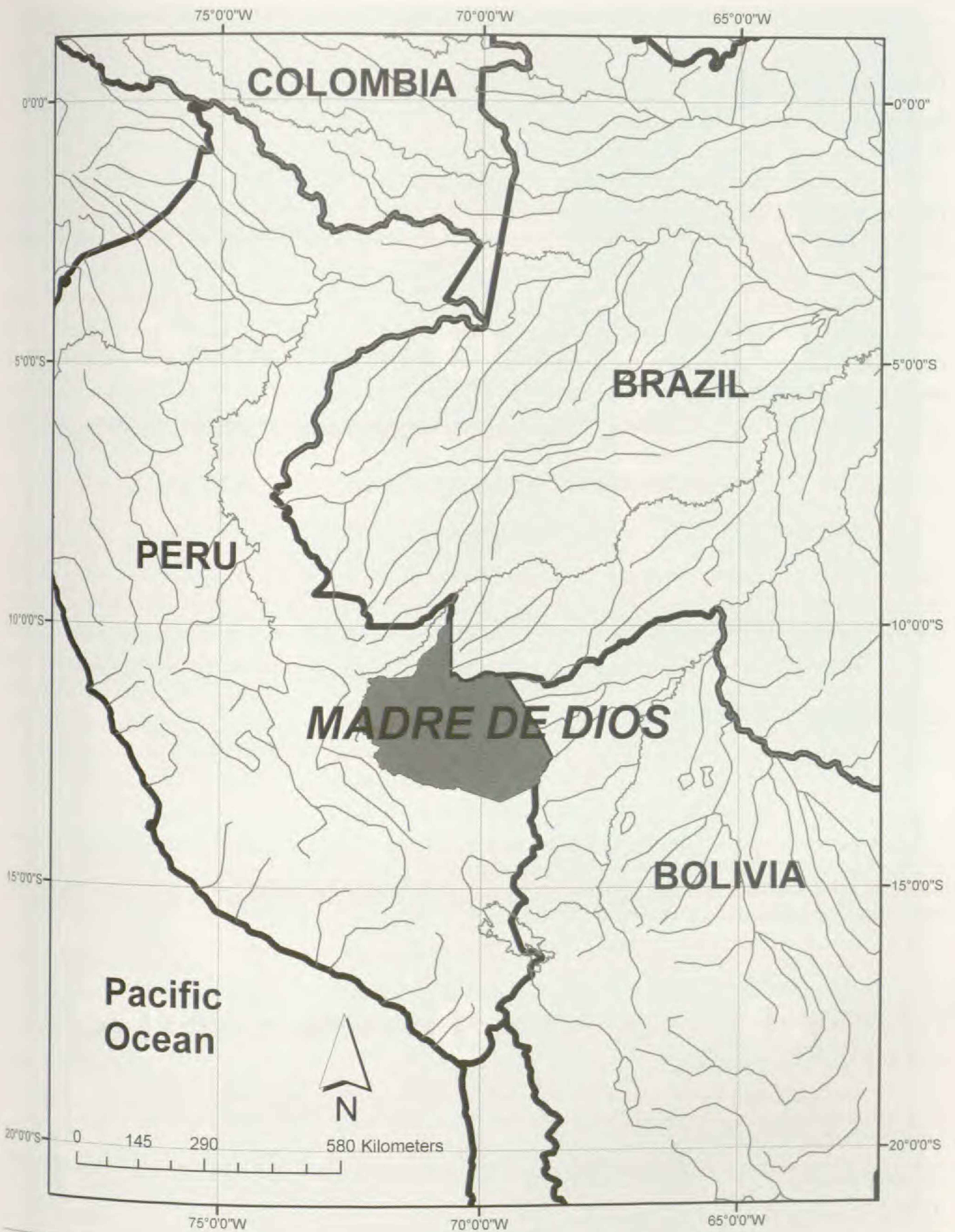


Fig. 1. Location of study region.

Annual average rainfall ranges between approximately 2,000 and 3,500 mm. Rainfall is unevenly distributed throughout the year, with greater than 80% falling between October and April. Average daily temperature ranges from 21 to 26°C. Southerly cold fronts from Patagonia, known as "frijajes," are common from June through August, rapidly decreasing temperatures by 10°C or more in a matter of minutes;

sustained for a period of several days, temperatures as low as 10°C have been reported. Climate data since 2001 is made available by the Amazon Conservation Association through the weather module of the Atrium Biodiversity Information System at BRIT (<http://atrium.andesamazon.org>).

Specimen and Data Collection

Between July 2005 and August 2009, approximately 70 km of line and trail-based transects were surveyed in 28 separate wetlands throughout Madre de Dios. Transects varied in length according to wetland size, ranging from 4 km in the largest wetlands, to 1 km in the smallest. All transects were oriented strategically to cross a diversity of wetland vegetation formations. Accessible populations of the most common *Vanilla* species were frequently monitored for phenological patterns. Opportunistic observations were made to document the activity of bees visiting flowers and fruits. If possible, photos and specimens of pollinators were collected for subsequent identification. Pollination rates for all species were estimated at the end of the flowering season by counting the number of empty floral bracts and fruits. Descriptions of floral scents were facilitated by enclosing the entire flower in a plastic film container for five minutes to intensify the fragrance. Plant specimens were collected in duplicate sets and deposited at the San Marcos Herbarium (USM) in Lima, Peru, and the BRIT Herbarium. Fresh flowers and fruits from each collection were photographed and preserved in 90% alcohol for descriptive studies.

RESULTS

Six species of *Vanilla* were encountered and documented in the wetlands of Madre de Dios. The following key is based primarily on morphological characteristics that are most useful in the field. Several species are notoriously variable in their morphology but proper identifications are not difficult even in sterile condition using a combination of vegetative and ecological characteristics. Climbing individuals attached to a host are generally much easier to key out and identify in the field than are scrambling vines. The key is followed by morphological descriptions of each species with notes about nomenclature, distribution, habitat, and natural history.

KEY TO SPECIES

1. Leaves membranaceous, thin, rostellum absent, flowers not resupinate _____ **1. *V. guianensis***
1. Leaves succulent, thick, rostellum present, flowers resupinate.
 2. Leaves narrowly lanceolate, sepals green _____ **2. *V. riberoi***
 2. Leaves ovate, obovate, or elliptic, possibly highly variable even on same vine, sepals yellow or red-brown.
 3. Stems > 1 cm in diameter, generally a massive terrestrial vine up to 20 m, raceme strictly axillary _____ **3. *V. pompona* subsp. *grandiflora***
 3. Stems < 1 cm in diameter, short (< 5 m in length) vine or epiphyte, racemes terminal and axillary on same plant.
 4. Leaves obovate with cuspidate apex, generally held horizontal to ground, always terrestrial vine, callus compact _____ **4. *V. cristato-callosa***
 4. Leaves ovate to elliptic with acute apex, mostly epiphytic, callus diffuse or absent.
 5. Leaves petiolate, discolorous with pale red-brown outline, internode length > than leaf length, sepals red-brown _____ **5. *V. bicolor***
 5. Leaves sessile, entirely green, internode length < than leaf length, sepals yellow _____ **6. *V. palmarum***

1. *Vanilla guianensis* Splitg. (Fig. 2a).

Plant a vine, occasionally reaching up to 10 m. Stems thin, brittle, ca. 0.4–0.7 cm in diameter, internodes 8–10 cm long, one to many-branched. Aerial roots short, thin, ca. 0.2 × 3 cm, unbranched. Terrestrial roots emerging from lower nodes and entering superficially into substrate, branched underground. Leaves alternate, produced from each node opposite to roots, distichous, thin and membranaceous; blade elliptic, ca. 3.7–11 cm wide and 7.5–22 cm long, green, apex acute-attenuate, margins entire. Inflorescences axillary, racemose, sessile, 2–20 flowered, fleshy, green; bracts triangular, ca. 1 cm long, green; pedicel ca. 0.3 cm wide and 3 cm long (pedicel of auto-pollinating individuals may be longer because fruit development begins

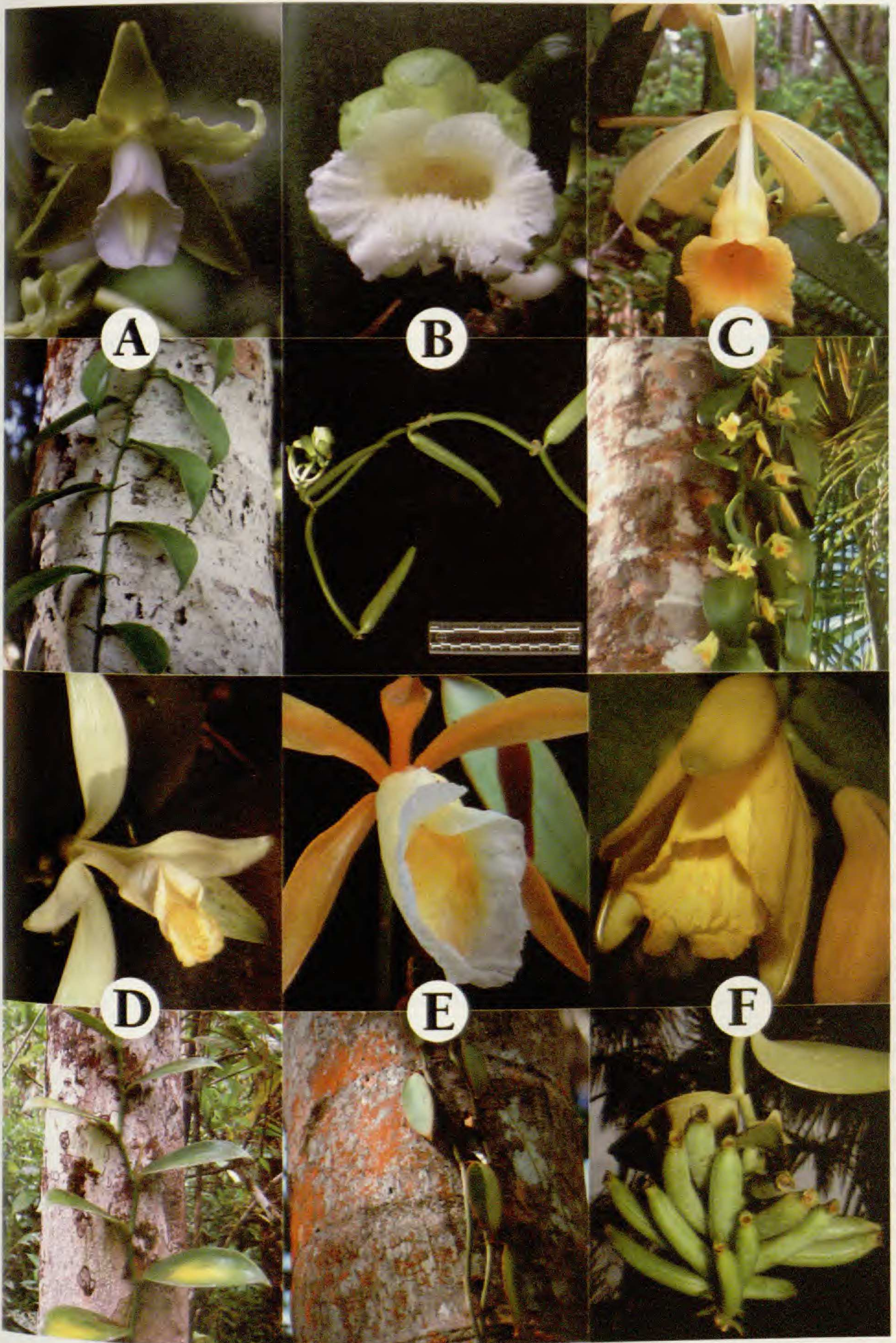


FIG. 2. Images of *Vanilla* species flowers (top) and vines in their natural habitat (below). A. *V. guianensis*. B. *V. riberoi*. C. *V. pompona* subsp. *grandiflora*. D. *V. cristato-callosa*. E. *V. bicolor*. F. *V. palmarum*.

in bud stage), pale yellow-green in color. Flowers not resupinate, fleshy, very stiff, ca. 7 cm wide, distichous on raceme, slightly fragrant (like freshly cut grass or trunk slash); buds green; sepals elliptic, undulate, ca. 1.7×4 cm, green, apex acute, margins keeled; petals elliptic, often strongly recurved, undulate or not, ca. 1.2×4 cm, green, apex acute; lip stiff, white, glabrous, forming triangular opening when fresh, attached to column on dorsal side for 0.4 cm of length, when flattened broadly pentagonal in shape, distinctly three-lobed; middle lobe 3 cm long, adaxial surface with distinctive yellowish channel formed from two broadly raised longitudinal keels, abaxial surface with distinct longitudinal furrow; lateral lobes white, ca. 1.8 cm long, stiff; callus absent; column 2.4 cm long, 0.4 cm wide, stiff, forks 0.4 cm from tip of stigma, upper fork holds anther ca. 0.3 cm beyond stigma; rostellum absent; anther ca. 0.2×0.2 cm with red-orange margins; stigma ca. 0.05×0.2 cm, with four nipple-like projections. Fruit dehiscent, cylindrical, ca. 1×18 cm, green and brittle when immature, splitting longitudinally along sutures, splitting valves turn dark brown, pliable, leathery, revealing seeds within a somewhat oily mesocarp, with disagreeable fragrance when moist.

Notes.—This species has a complicated nomenclature, with no type specimen and several synonyms. The oldest name is *V. guianensis* Splitg. and thus conserved. However, it may also be found as *V. acuta* Rolfe, *V. latisegmenta* Ames, and *V. surinamensis* Rchb. f. (Soto-Arenas & Cribbs 2010). Soto-Arenas and Cribbs (2010) place it in subgenus *Vanilla*, subsection *Membranaceae*, a group characterized by its thin leaves, continuous endoderm, large number of row fibers in the stem, and little differentiation between vegetative and reproductive axes (Soto-Arenas 2003).

Habitat and Distribution.—This species is relatively common throughout the Amazon basin (Soto-Arenas, pers. comm.). Although in our study region it occurs more abundantly in association with *M. flexuosa* wetlands, it is the only species not strictly restricted to wetlands. For example, we have documented individuals growing in managed banana plantations, suggesting that it is a fast-growing, colonizing species. In *M. flexuosa* wetlands with deep histosols and acidic waters it generally prefers areas with abundant, low-lying, shrubby trees common to wetlands, such as *Ilex* sp. (Aquifoliaceae), *Tapirira guianensis* (Anacardiaceae), and *Tabebuia insignis* (Bignoniaceae). The leaf litter of these common, non-palm wetland trees may be important in seedling germination.

Natural History.—Flowering phenology is somewhat sporadic; various individuals flowered in January, April, May, and November during 2005–2006. The number of flowers per individual ranged from 5 to about 50, depending on plant size. Flowers often open in triplets and remain open for three to seven days as observed for other membranaceous species (Soto-Arenas et al. 2003). Due to longer flower longevity and rapid rates of anthesis a large floral display often accumulates on reproductive branches. The most gregariously flowering branches are almost always those that are pendent, hanging from the main vegetative axis.

Vanilla guianensis is apparently self-pollinated at early anthesis as the stigma and anther grow to contact one another. Pollination rates are approximately 78% (Table 1). No potential pollinators have been observed, but Soto-Arenas (2003) suggests that the stiff flowers and relatively closed throat of *V. guianensis* may be adapted to large, strong pollinators such as carpenter bees (*Xylocopa* spp). However, no potential pollinators have been observed near flowers of *V. guianensis* in wetlands.

Unlike other *Vanilla* species, the flower and column of *V. guianensis* rapidly abscise from the developing fruit. Once mature, dehiscent fruits have a rather unpleasant, putrid odor for one to several days. While such odors may be attractive to some animal dispersers, none, however, have been observed near fruits. The separated valves may remain oily and pliable for several weeks and when dry become leathery. The thin fibrous stems do not readily propagate vegetatively in artificial settings.

2. *Vanilla riberoi* Hoehne (Fig. 2b).

Plant a vine, generally loosely climbing on understory trees. Stems dark green, succulent, ca. 0.5–0.8 cm in diameter, internodes 10–15 cm long. Aerial roots produced from each node, short, stout, white, unbranched. Terrestrial roots emerging from lower nodes and entering superficially into substrate, branched and extensive underground. Leaves alternate, produced from each node opposite to roots, distichous, held at 0 to 15 degrees below horizontal, succulent; blade narrowly lanceolate-linear, ca. 1.5–2 cm wide and 8.5–14 cm

TABLE 1. Pollination rates of each *Vanilla* species. Rates were calculated as the total number of fruits divided by the total number of bracts. Counts were timed at the end of the flowering season. **Auto-pollination was tested by placing 1mm mesh bags over racemes.

| Species | Counts | | | | Pollination rates % | Pollination mechanism |
|-------------------------------|--------|--------|----------------|-------------|---------------------|-----------------------|
| | Bracts | Fruits | Racemes | Individuals | | |
| <i>V. bicolor</i> | 31 | 22 | 13 | 13 | 71 | auto** |
| <i>V. palmarum</i> | 37 | 26 | 3 | 3 | 70.3 | auto |
| <i>V. guianensis</i> | 163 | 127 | 38 | 8 | 78 | auto |
| <i>V. pompona grandiflora</i> | 5405 | 50 | Not calculated | 148 | 0.9 | <i>Eul. meriana</i> |
| <i>V. cristato-callosa</i> | 209 | 14 | 16 | 12 | 6.6 | Euglossine |
| <i>V. riberoi</i> | 88 | 1 | 12 | 3 | 1.1 | Euglossine |

long, dark green when fresh, texture smooth, apex acute, margin entire. Inflorescences axillary only, racemose, fleshy, green, sessile ca. 1 to 20-flowered; bracts triangular, ca. 1.8 cm long and 1 cm wide, green, non-floriferous bracts generally two; pedicel ca. 0.5 × 4.5 cm, white at base to three-quarters length then fading to green. Flowers resupinate, somewhat stiff, fleshy, span ca. 4–5 cm, arranged spirally, non-fragrant; buds green; dorsal sepal oblanceolate, ca. 1 × 5 cm, green, apex rounded; lateral sepals oblanceolate, ca. 1.4 × 4.7 cm, green, apex rounded; petals linear, ca. 1 × 4.6 cm, green, ribbed dorsally; lip saccate when fresh, reflexed, stout, ca. 3.8 cm long, white, fused with column for two-thirds length dorsally, flabellate when flattened, unguiculate, the claw of white hirsute-papillose hairs forming patch ca. 1.5 × 1 cm on opening of ventral surface, margin revolute; callus wide, ca. 0.5 × 0.4 cm, penicillate with wide lacinate scales; column strongly concave, ca. 2.7 cm long, 0.4 cm wide, adaxial surface hirsute; rostellum thick, wide; stigmatic surface two-lobed. Fruit dehiscent, cylindrical in cross-section, green and brittle when immature, splitting longitudinally along sutures, splitting valves turning dark brown, pliable, revealing seeds in somewhat oily mesocarp, pleasantly fragrant.

Notes.—Soto-Arenas and Cribb (2010) place *V. riberoi* in subgenus *Xanata*, section *Xanata*.

Habitat and Distribution.—This species has been previously collected from inundated areas of Mato Grosso, Brazil, near the Bolivian border, Columbia, and Guyana. Of the indigenous terrestrial *Vanilla* species in Madre de Dios, it is the most tolerant of substantial water level fluctuations and we have documented its presence in at least four habitats, all with varying flood regimes: permanently inundated *M. flexuosa* wetlands on histosols, aseasonally inundated *M. flexuosa* wetlands on gleysols, seasonally inundated *shebonales* dominated by *Attalea* sp. (Arecaceae), and small forest patches (usually in association with arborescent palms) characterized by clayey soils that retain water after precipitation events. Although this is one of two *Vanilla* species not restricted to *M. flexuosa* wetlands, it is restricted to areas with hydromorphic soils.

Natural History and Reproduction.—The flowering season occurs in mid-August to September, just prior to the main flowering season of *V. pompona* subsp. *grandiflora*, and their phenologies partially overlap. Ephemeral flowers open singly and last a single day. Pollination rates are low, estimated to be about 1% based on three fertile individuals studied (Table 1). Nothing is known about pollinators, but such low pollination rates suggest outcrossing by insect vectors, probably Euglossine bees.

3. *Vanilla pompona* Schiede subsp. **grandiflora** (Lindl.) Soto-Arenas (Fig. 2c).

Plant a robust, succulent vine climbing up to 30 m. Stems green, thick, succulent, ca. 0.9–2.3 cm in diameter; internodes 9–13 cm long for climbing individuals, one to many-branched, when tissues are damaged the sap is slightly irritating when rubbed. Aerial roots produced from each node, short, stout, white, unbranched, ca. 0.5 cm in cross-section, ca. 3–5 cm long. Terrestrial roots emerging from lower nodes and entering superficially into substrate where branched and extensive. Leaves alternate, produced from each node opposite to roots, distichous, held at 30 to 60 degrees below horizontal, succulent, sessile; blade highly variable in size and shape, elliptic to suborbicular, ca. 3–13 cm wide and 6–30 cm long, texture smooth, apex slightly cuspidate to rounded, margin entire. Inflorescences axillary, racemose, fleshy, green, sessile,

ca. 1 to 20-flowered; bracts triangular, ca. 1.5 cm long, green; pedicel green, persistent on maturing fruit. Flowers resupinate, tender, fleshy, span ca. 15 cm wide, arranged spirally, fragrant or not, remaining attached to ovary if successfully pollinated; buds green; dorsal sepal oblanceolate, reflexed when fully open, ca. 1.5 × 9.4 cm, yellow; lateral sepals oblanceolate, reflexed, ca. 1.5 × 8.5 cm, yellow; petals oblanceolate, reflexed, ca. 1.1 × 9 cm, yellow, with thickened midvein on dorsal surface; lip somewhat saccate when fresh, fused with column for ca. 5 cm, uniformly yellow except for a characteristic pale, triangular discoloration on ventral surface of opening, flabellate and almost triangular when flattened, margins slightly revolute, pleated, unguiculate, the claw caniculate with dark yellow rows of trichomes running longitudinally between lip margin and callus, ca. 2.2 cm long and 0.3 cm wide; callus well-developed, ca. 0.8 × 0.6 cm, penicillate with lacinate scales; column ca. 6.3 cm long, 0.4 cm wide, hirsute on ventral surface near rostellum gradually becoming glabrous; rostellum broad, thick, yellow. Fruit dehiscent, ca. 2.6 × 15 cm, fleshy, triangular in cross-section, green and brittle when immature, splitting longitudinally along sutures into unequal valves at maturity, split ends turn pliable, leathery and brown-black in color, revealing seeds embedded within an extremely oily mesocarp and emitting strong vanillin fragrance.

Notes.—*Vanilla pompona* subsp. *grandiflora* is a member of the subgenus *Xanata*, section *Xanata*. New molecular data suggest that the *V. pompona* of Mexico is nested within the variable *V. grandiflora*, but the older name, *V. pompona*, is retained (Soto-Arenas pers. comm.). The species complex is quite variable and several disjunctions are evident within its widespread distribution (Soto-Arenas & Dressler 2010). The original species described by Schiede, now *V. pompona* Schiede subsp. *pompona*, is a narrow endemic on the Mexico/Guatemala border and all records of its existence in South America are wrong.

Distribution and Habitat.—*Vanilla pompona* subsp. *grandiflora* is widely distributed from Honduras to Bolivia (Soto Arenas pers. comm.). In Madre de Dios it is mostly restricted to open, flooded savannah habitat within *Mauritia flexuosa* wetlands, characterized by deep, permanently saturated histosols and minimal water level fluctuations. While the vine is robust and resilient to frequent disturbances caused by falling palm fronds, its roots are vulnerable to even short periods of inundation. Within its habitat it is generally restricted to small hummocks formed by the accumulation of *M. flexuosa* frond mulch. It often forms dense populations over extensive areas where conditions are favorable.

Natural History.—On a given inflorescence flowers open singly every two to three days. Flowers open as early as 3:00 am and generally last 12–15 hours, wilting with the afternoon heat. Individuals tend to flower more profusely immediately following small-scale (5 C° or less are sufficient) temperature reductions (i.e., *friajes*). During these cool weather spells, up to two flowers may open per inflorescence and we have observed displays of over 30 open flowers on a single individual. Flowering responses to temperature seem to be facilitated by determinant racemes with buds almost fully developed prior to the initiation of the flowering season. Several of the most fully developed, basally located buds may be poised to open during unpredictable cool spells. The response to cool temperatures is general and immediately following *friajes* the entire population may not flower for one to several days while apically located buds develop. The maximum number of flowers observed on a single individual throughout an entire season was 200. Flowering phenology is bimodal, with two rather short flowering episodes of approximately 30 days each in April and September/October. Significantly more individuals flower during the September/October season, probably in response to the long dry season commencing in June/July.

The flowers produce a “sweet” fragrance, but this is sometimes barely perceptible and the potency varies between individuals. Particularly fragrant flowers attracted two species of Euglossine bees, *Euleama meriana* and *Euglossa imperialis*. Several individuals of both species may repeatedly circle a single fragrant flower for several minutes, often demonstrating antagonistic behavior. The smaller, and generally more numerous *Eug. imperialis* is the more aggressive species, however its small size probably precludes it as an actual pollinator. We have observed only *Eul. meriana* to pollinate flowers on two occasions. In both cases a solitary bee entered the floral tube for two to four seconds and with no delay departed along a straight line track. Collection of fragrance of floral origins has never been observed, suggesting that flowers are deceptively pollinated (see Lubinsky et al. (2006) for a more detailed description).

Pollination rates are extremely low, measured at less than 1% in September 2005 (Table 1). The number of fruits per individual ranged from one to four, the great majority of fruiting individuals producing only a single fruit during any given season. Fruits mature and begin to dehisce approximately five to nine months after pollination and open slowly over a period of approximately two weeks, revealing thousands of tiny seeds embedded within an extremely oily mesocarp. The green, brittle fruit turns dark brown and pliable as it opens. This process begins at the fruit apex and is usually preceded by a slight yellowing of the exocarp. Mature (dehiscing) fruits have a sweet vanilla aroma. Fruit fragrance is attractive to a limited number of bee species, interestingly including the two Euglossine species attracted to floral fragrance, *Eul. meriana* and *Eug. imperialis*. Both species demonstrate typical fragrance collection behavior (see Dressler (1968) for a detailed description of fragrance collection behavior) and may remain at a single fruit for over 15 minutes. While they may land on any part of the fruit, there seems to be intense competition for the most recently opened (probably most fragrant) section. Other common bee visitors include a single species of stingless bee (*Trigona* sp.), and one species of carpenter bee (*Xylocopa* sp.). The species of *Trigona* has been observed to collect and fly away with small packets of twenty seeds on their hind tibia. Although not confirmed, the tiny seeds embedded in the fragrant, oily mesocarp may also be intentionally collected by the Euglossine bees during fragrance collection. Nothing is known about the fate of these seeds once collected, however we have often observed *Trigona* bees dropping their seed packets. Occasional herbivory (entire fruits or sporadic nibbles) of dehiscent fruits suggests that larger vertebrates, such as bats or locally abundant marsupials, may also be important dispersers, but we have never made direct observations.

Seedling emergence is distinctly seasonal. Most seedlings surface in May, coinciding with the initiation of the dry season. However, seedlings are extremely rare and most reproduction is through vegetative propagation. The vine is extremely clonal and vigorous-growing; monthly growth rates often exceed one meter. Frequent disturbances due to falling palm fronds often topple vines fragmenting them in the process. Fragmented sections readily sprout vegetative buds and in this manner form locally dense, clonal populations.

This *Vanilla* species demonstrates a degree of myrmecology, especially during bud maturation. Small *Azteca* ant colonies anticipate the production of sugars exuded at the abscission layer of immature buds by building colonies in the small, circular depressions housing the axillary meristems.

4. *Vanilla cristato-callosa* Hoehne (Fig. 2d).

Plant an understory vine climbing to 4 m. Stems succulent, ca. 0.6–0.9 cm in diameter, internodes ca. 6 cm long for climbing individuals, rarely branched. Aerial roots produced from each node, white, unbranched. Terrestrial roots emerging from lower nodes and entering superficially into substrate, branched and extensive underground. Leaves alternate, produced from each node opposite to roots, distichous, held horizontal to ground, succulent, sessile; blade obovate to elliptic, ca. 3–7 cm wide and 9.5–17 cm long, color often green-yellow when fresh, texture smooth, apex cuspidate, margin entire. Inflorescences terminal or axillary, racemose, fleshy, green, sessile, ca. 1 to 40-flowered; bracts triangular, ca. 0.5 cm long, green; pedicel ca. 0.4 cm wide and 4.9 cm long, white for half its length and fading to green apically. Flowers resupinate, tender, fleshy, arranged spirally, fragrance “fabaceous” (like torn leaf of a bean); buds green; sepals oblanceolate, ca. 0.9 × 6.3 cm, yellow, apex acute; petals oblanceolate, ca. 0.8 × 5.6 cm, yellow, apex acute; lip narrowly tubular when fresh, ca. 5.5 cm long, fused with column for 4 cm dorsally, yellow, flabellate when flattened, unguiculate, the claw a patch of papillae-like projections ca. 0.6 × 1 cm dominating ventral surface near opening; callus penicillate, distinct, ca. 0.4 × 0.3 cm, yellow lacinate scales; column sinusoidal, 4.6 cm long, 0.2 cm wide; anther ca. 0.2 × 0.4 cm, yellow. Fruit dehiscent, cylindrical in cross-section, ca. 1 × 15 cm, green and brittle when immature, splitting valves turning brown, leathery, oil rich, often producing abundant gelatinous substance as it opens, with strong vanillin fragrance.

Notes.—An obscure and little known complex, probably synonymous with *V. cristagallii* Hoehne, the main difference apparently in flower size (Soto-Arenas & Cribb 2010). Hoehne proposed several names, but

the drawings and type specimens are not useful (Soto Arenas, pers. comm.). These represent a diverse group of poorly collected Amazonian species and field work is necessary to resolve species concepts. Soto-Arenas and Cribb (2010) place it within subgenus *Xanata*, section *Xanata*.

Habitat and Distribution.—Only two fertile collections possessing flowers are known and they are both from the Peruvian Amazon (Soto Arenas, pers. comm.). In our region *V. cristato-callosa* occurs in *M. flexuosa* wetlands characterized by deep histosols where it exhibits a patchy distribution, occurring in small populations within localized areas. Generally, the species is more tolerant of lower light conditions than other local *Vanilla* species.

Natural History.—Flowering occurs in mid-January to April, during the height of the rainy season. In agricultural settings where resource limitations are reduced the flowering season is greatly extended several months. In this case, the terminal racemes prevent upward growth and the vine remains vertically stunted. Ephemeral flowers open singly over an interval of two to four days. Pollination rates are approximately 6% (Table 1). The pollinator is unknown.

Fruits of reproductive individuals in their natural habitat often occupy a terminal position on the inflorescence, suggesting that once pollinated, continued flower production ceases. Fruits mature in approximately six months. Green, brittle fruits turn pliable and oily during dehiscence, a transformation that begins at the tips of newly separated valves and progressively moves upward. In this species a gelatinous substance is sometimes present at the confluence of the valves as they separate. Dehiscent fruits are oily with a strong vanilla aroma, somewhat spicy and cinnamon-like. On several accounts we observed a few individuals of a single species of metallic green *Euglossa* sp. visiting old, completely opened fruits and demonstrating typical fragrance collection behavior (Roubik 1989). The species exhibits a degree of myrmecology, as ants that feed on a sugary exudates secreted at the abscission line between bud and ovary are often present during bud and raceme development.

5. *Vanilla bicolor* Lindl. (Fig. 2e).

Plant a vining epiphytic herb in crowns of *Mauritia flexuosa*. Stems thin, ca. 0.4 cm in diameter, green; internodes 8.5–10.5 cm long. Aerial roots produced from each node, attached to host, thin, ca. 3–100 cm in length, sometimes few-branched at apical end, tannish in color. Leaves alternate, produced from each node opposite to roots, distichous, drooping from long petioles; petiole slightly caniculate, ca. 1 cm long, dark red-brown; leaf blade elliptic to slightly ovate, ca. 2.5–4.5 cm wide and 5–11 cm long, discolorous, with pale-green central area and pale red-brown outline along margins, succulent, texture smooth, apex acute, margin entire. Inflorescences axillary and terminal, racemose, fleshy, green, sessile, one to 20 per individual, ca. 1 to 10-flowered; bracts cymbiform, ca. 0.3 cm wide and 0.6 cm long, color red-brown, non-floriferous bracts generally two; pedicel ca. 3 cm long and 0.2 cm in diameter, dark red when young, maturing to green. Flowers resupinate, fleshy, tender, 10 cm across, arranged spirally on raceme, non-fragrant, remaining attached to ovary if successfully pollinated; buds deep red-brown; dorsal sepal oblanceolate, ca. 0.7 × 7.5 cm, orange-brown; lateral sepals oblanceolate, ca. 0.9 × 7.5 cm, orange-brown; petals oblanceolate-linear, ca. 0.6 × 6.5 cm, very pale orange-brown; lip trumpet-like when fresh, fused with column for three quarters of its length, exterior ringed white around mouth fading to yellowish-orange towards interior, margins entire, flabellate and almost triangular when flattened, unguiculate, the claw of soft, yellow tomentose-papillose hairs near apex merging with short yellow pubescence in interior and callus; callus diffuse, ca. 0.7 × 0.3 cm, with thick yellow tomentose; column straight, ca. 4.2 cm long and 0.2 cm wide, ventral surface with lanuginous-hirsute hairs for about a third of its length distally, then glabrous; rostellum extremely thin, narrow, pale white; anther ca. 0.3 × 0.4 cm. Fruit dehiscent, cylindrical, ca. 10 cm long, when immature brittle and brownish red or green, splits longitudinally along sutures, splitting valves turning black, pliable, leathery, revealing seeds embedded in a scarcely oily mesocarp, non-fragrant.

Notes.—*Vanilla bicolor* has been generally known by its later synonym, *V. wrightii* Rchb. F. (Christenson 1995). It differs from all other American *Vanilla* (except for the membranaceous group [*V. guianensis*]), in that

the penicillate callus is not compact, but rather diffuse. Soto-Arenas and Cribb (2010) placed it in subgenus *Xanata* section *Xanata*.

Distribution and Habitat.—This species has a wide distribution, previously being collected in Cuba, Ecuador, British Guyana, and Venezuela (Soto-Arenas & Cribb 2010). This is the first documentation of *V. bicolor* in Peru, significantly extending its range to the south. In our region it is a common epiphyte of *Mauritia flexuosa*. Long, slender roots reach deep into the slender pocket formed between the sheathing petiole bases of palm fronds and the trunk. It is largely restricted to specific wetland habitat characterized by deep histosols and acidic waters. The species is occasionally encountered as a short terrestrial vine in very open areas with high insolation. These uncommon individuals reach maximum heights of 3 to 4 m well below canopy level and never gain epiphytic status in *M. flexuosa* crowns. Terrestrially rooted individuals likely result from the clonal propagation of fallen epiphytes rather than seedling germination and represent the exception, rather than the rule, thus we maintain its classification as a true epiphyte, at least in our region. That said, at Kaieteur National Park, Guyana, the species is known to scramble across rocks at ground surface.

Natural History.—The flowers of *V. bicolor* are non-fragrant, open singly at approximately five-day intervals, and last less than 24 hours. Flowering phenology is fairly aseasonal. We have observed flowers during all 12 months of the year, although there seems to be a slight peak in August during the height of the dry season.

Pollination rates are extremely high, falling within the range of 45 to 75% (Table 1). No local pollinators have been observed at or near flowers and bagging experiments suggest that the plant is self-pollinating. Self-pollination seems to be achieved by the secretion of excess stigmatic fluids that creates a mixture of moisture and pollen grains. The rather thin, narrow rostellum is an ineffective barrier between the pollen-fluid mixture and the stigmatic surface, greatly facilitating self-pollination through excessive stigmatic leak.

Fruiting phenology is aseasonal. Mature fruits, which are quick-drying and non-oily, can be observed throughout the year. The thin, leathery capsule opens from below over the course of several days. The splitting halves turn black as they dry, however they remain pliable for some time. Seeds are not held in a particularly oily matrix as in other fragrant species. The mechanism of seed dispersal of *V. bicolor* is unknown. Lack of fragrance, oils, or sugars, presence of extremely small seeds, and its canopy habitat are all suggestive of dispersal by a mixture of wind turbulence and gravity. As the fruits dehisce and dry, the seeds are exposed to strong winds and then fall downward. Seedlings are abundant, germinating almost exclusively in the small openings between palm trunks and the sheathing petiole bases of palm fronds. This species is not easily propagated vegetatively in artificial settings.

6. *Vanilla palmarum* Lindl. (Fig. 2f).

Obligate epiphyte on *Mauritia flexuosa*. Stems succulent, ca. 0.5 cm in diameter, green, internodes 5–6 cm for climbing individuals, one to many-branched. When reproductive often forming a long shoot with slightly diminishing leaf size and internode length. Aerial roots produced from each node, either short (less than 2 cm) and cup-like on reproductive shoots or long and thin on vegetative shoots. Leaves alternate, produced from each node opposite to roots, distichous, sessile, succulent; blade elliptic to ovate, ca. 3.2–6 cm wide and 7–16 cm long, color light green, texture smooth, apex acute to acuminate, margin entire. Inflorescences mostly terminal, racemose, fleshy, green, ca. 5 to 15-flowered; bracts either foliaceous or cymbiform; foliaceous bracts located at inflorescence base, elliptic, ca. 3 cm long, apex acute, generally two, occasionally non-floriferous; cymbiform bracts above, ca. 0.5 cm long, green, always floriferous; pedicel green, but somewhat whitish at extreme base. Flowers resupinate, tender, fleshy, arranged spirally, flowers lightly fragrant, remaining attached to ovary if successfully pollinated; buds green; dorsal sepal elliptic, ca. 1.2 × 6 cm, yellow, apex acute; lateral sepals slightly falcate with bend beginning 2.5 cm from base, ca. 1.3 × 5.6 cm, yellow; petals elliptic, ca. 1.6 × 5.5 cm, yellow, apex acute, longitudinally ribbed on dorsal surface; lip

largely pentagonal when flattened, uniformly yellow, unguiculate, the claw of 6–7 longitudinal ridges formed by conspicuous swollen tissues, margins undulate; callus absent; column slightly convex, ca. 4 cm long and 0.25 cm wide, hirsute on ventral surface near rostellum; rostellum somewhat thick, yellow. Fruit dehiscent, triangular in cross-section, green and brittle when immature, ca. 12 cm long, splitting longitudinally in two unequal valves at maturity, valves turning dark brown, pliable, leathery, revealing seeds embedded in a scarcely-oily mesocarp, non fragrant.

Notes.—*Vanilla palmarum* belongs to subgenus *Xanata*, section *Xanata*. It differs from all other species within the group in lacking a penicillate callus (Soto-Arenas & Cribb 2010).

Habitat and Distribution.—*Vanilla palmarum* is widespread in Madre de Dios, occurring in the small but ubiquitous *Mauritia flexuosa*-dominated wetlands characterized by hydromorphic substrates with a high mineral component. The species has been observed in wide (approximately 200 m) spring-fed streams with sandy bottoms, on unconsolidated clays on the edges of spring-fed blackwater lakes, and in rain-fed depressions on gleysols. In all cases *M. flexuosa* was monodominant. Similar to *V. bicolor*, the vining herbs are epiphytic in *M. flexuosa* crowns, sending long, slender, branched roots deep into the sheathing petioles. Although restricted to the same host, *V. palmarum* and *V. bicolor* never occur in mixed populations, the latter restricted to *M. flexuosa* wetlands with thick, accumulated organic material.

This species is also known from the Guianas where it also grows in the crowns of *Mauritia flexuosa*. It is also reported to occur commonly in northeastern Brazil and in Mato Grosso, Brazil, where it grows on *Syagrus coronata* (Arecaceae), a common arborescent palm of drier 'cerrado' formations (Toscano de Brito, pers. comm.). Other possible hosts include species of the palm genera *Orbigyna*, *Attalea*, and *Scheelea* (Soto-Arenas & Cribb 2010).

Natural History.—Flowers open singly on the racemes at intervals of three to four days. Flowering phenology is bimodal, with peaks in January to February and October to November. The flowers are slightly fragrant but no potential pollinators have been observed near flowers. Pollination rates are high at 76%, apparently resulting from self-pollination (Table 1). Despite a seemingly more effective barrier provided by the thick rostellum, the mechanism of self-pollination seems to be identical to that of *V. bicolor*. Excessive stigmatic fluids induce pollen grains to leak onto the extreme lateral margins of the stigmatic surface. Pollination rates of flowers located basally on racemes are significantly higher than flowers located apically. This may indicate a degree of control of the self-pollination mechanism, perhaps induced by high resource requirements of fruit maturation and mediated by the allocation of limited resources to competing vegetative and reproductive needs (Chiariello & Gulman 1991). The fruits are non-fragrant and dehisce over the course of several days. Although significantly thicker than *V. bicolor* the fruit mesocarp is not particularly oily and the two valves rapidly dry within weeks, turning leathery. Seedlings are abundant in the canopies of *M. flexuosa* palms as in *V. bicolor*. Reproductive adults high in the canopy probably seed the very specialized germination microsites through combination of wind turbulence and gravity.

DISCUSSION

Wetlands and *Vanilla*

This work represents the accumulation of about seven years of data from field investigations of *Vanilla* orchids in the wetlands of Madre de Dios. Early in our investigations we directed our attention to wetland habitat as *Vanilla* showed distinct preferences for hydromorphic conditions. In the area, the genus generally occurs in association with *Mauritia flexuosa*, or the "aguaje" palm as it is known locally in Peru. The palm is indicative of hydromorphic soils in topographical depressions and often forms monodominant stands, or "aguajales" (Kahn 1988). Substrates, vegetation structure, and flora vary according to water source and hydrological parameters, but all *M. flexuosa* formations are characterized by: (1) very low sediment loads during relatively brief periods of inundation, (2) relatively minor water level fluctuations (less than 50 cm), and (3) low canopies with greater light penetration into the subcanopy (Kahn et al. 1993). Relatively higher insolation and stable hydrological parameters favor the establishment of vining *Vanilla* species, which have precarious

seedling stages in the understory and, as adults, superficial root systems vulnerable to prolonged flooding. Under these conditions *Vanilla* often occurs in dense populations and is one of the most conspicuous elements of wetland vegetation. For example, in a related study concerning the distribution patterns of *Vanilla* in regional wetlands, approximately 60% of points placed systematically throughout 70 km of line transect in 28 wetlands, contained at least one species of *Vanilla*, although up to four species occurred at the same point within a 30 m radius. *Vanilla pompona* subsp. *grandiflora* alone was present in over 40% of points and has population densities exceeding 250 individual ramets per hectare (Householder, unpublished data).

While we have collected over 50 species of orchid associated with *Mauritia* wetlands, surprisingly few other orchid taxa are found on *M. flexuosa* trunks, probably the result of the challenges of frequent disturbances created by falling palm fronds, slow growth of epiphytic orchids (Zotz 1995), and lack of suitable germination sites on the bare, smooth *Mauritia* trunks (Nieder et al. 2000). Within the Orchidaceae, the vining habit is unique to the genus *Vanilla* (Dressler 1993), and the habit's role in palm-dominated wetlands is noteworthy. All of the epiphytes are obligate to *M. flexuosa* and their vining habit allows individuals to maintain their canopy positions by occupying new fronds as senescing ones are sloughed. Unlike the epiphytes, *Vanilla* climbers are not restricted to *Mauritia* hosts, however the palm's shear dominance does make it their most common phorophyte. Climbing vines with terrestrial roots are able to maintain or quickly regain their elevated positions in the canopy after frequent disturbances caused by falling fronds. This level of adaptability may be extremely important in a constantly changing environment, especially if seed germination is limited (Price & Marshall 1999). In short, the success of *Vanilla* in *Mauritia*-dominated wetlands is likely a reflection of the shared ecological inclinations of both palm and orchid and the peculiar growth form of the orchid that provides resilience under a constant disturbance regime.

Fragrance and Bees Interactions

Three of the six *Vanilla* species of Madre de Dios possess pleasantly fragrant fruits. The fragrant condition is associated with succulent fruits with an oil-rich mesocarp and frequent visits by fragrance-collecting Euglossine bees. Hanging fruits slowly split into two separating valves over the course of days to weeks, depending on the species and environmental conditions (fruits in full sun seem to split faster). The splitting valves turn pliable and dark brown to black in color. The opening of the suture is usually preceded by a noticeable band of yellow discoloration that moves upwards as the valves separate. The intensity of fruit fragrance during dehiscence, even on the same fruit, is quite variable from day to day suggesting that the complex enzymatic reaction responsible for producing fruit fragrance may be in part environmentally influenced. The separate valves can remain pliable and moist for months due to abundant oils, turning progressively leathery as they dry out on the vine.

The dispersal mechanism(s) of *Vanilla* remains enigmatic; however several authors have suggested Euglossine bees or bats as potential dispersers (Madison 1981, Soto-Arenas 2003, Lubinsky et al. 2006). We observed *Trigona*, and possibly Euglossine bees, to form sticky seed packets which they often fly away with. Euglossine bees are well-known scent collectors; however the *Trigona* bees may have been more interested in the nutritional value of the oils. Herbivory, possibly due to vertebrate mammals, seems to be extremely rare. That said, the seeds are easily rubbed off and are extremely sticky due to a thin covering of oil. This covering may aid in epizoochorous forms of seed dispersal by any visitor, insect or vertebrate.

The adaptive value and evolutionary significance of fruit fragrance remain unexplored. Fruit fragrance, associated with an oily mesocarp, is a common trait amongst New World *Vanilla* (Soto-Arenas 2003) and it was clearly the main attractant for the Euglossine bee visitors. However, we were surprised by the apparent specificity of bees to fruits. Vanillin, one of the most important aromatics in the commercialization of *Vanilla* fruit, is a general attractant to dozens of Euglossine species in southeastern Peru (Pearson and Dressler 1985). Thus, the few species of bees lured to fragrant fruits of *V. pompona* subsp. *grandiflora* and *V. cristato-callosa* suggests that it is the less abundant aromatics or modifiers other than, or in combination with, vanillin that may be responsible for the observed specificity (Hills et al. 1972). Such phenomena have been well documented in orchid flowers pollinated by Euglossine bees (Adams 1966; Gerlach 2010) where

specific pollinator relationships, floral fragrance, and reproductive success are clearly linked (Dodson 1962; van der Pijl & Dodson 1966; Dodson et al. 1969; Hills et al. 1972). However, links between disperser specificity and reproductive success are less clear, at least in *Vanilla*. Curiously, in the case of *V. pompona* subsp. *grandiflora*, both flowers and fruits seem to attract the same Euglossine species, presumably due to the presence of similar aromatic compounds. The potential parallels between flower and fruit fragrance raise intriguing questions concerning the possible role of pollinator interactions in evolution of fruit fragrance of *Vanilla*. Thus, while we suspect that seed dispersal by bees (Madison 1981; Lubinsky et al. 2006), bats, or other animals is entirely possible, and that fragrance may indeed play an important role, we are unsure of the role that these disperser relationships may have played in the evolution of fruit fragrance.

Vanilla bicolor is expected to have fragrant fruits (Soto-Arenas et al. 2003). However, the relatively dry, non-oily fruits are odorless. The lack of fragrance is curious given its basal position within the clade of fragrant *Vanilla* (Soto-Arenas et al. 2003). Lubinsky (2006) and Dressler (1989) suggest that succulent, possibly fragrant fruits may be the ancestral condition in the genus. Madison (1981) suggests that a transition from bee dispersal (possibly associated with fruit fragrance) to wind dispersal (non-fragrant), would be a simple evolutionary step within the family. In any case, the evolution of fruit fragrance within the genus would be much enlightened by mapping its occurrence or disappearance on a phylogeny. However, neither detailed information concerning natural history nor a complete phylogeny of the genus exists.

Distribution Patterns

Vanilla is often considered to be a genus of habitat specialists, often restricted to small geographic ranges and high levels of endemism (Soto-Arenas et al. 2003). Dispersal mechanism(s) remain enigmatic, but *Vanilla* is notable for its smooth, crustose seeds with a well-developed endosperm (Garay 1986). These traits are highly atypical of the family with the majority of the 20,000–30,000 species possessing tiny, dust-like, highly corrugated seeds with little or no endosperm neatly adapted for wind dispersal (Dahlgren and Clifford 1983). Several authors, using evidence from observational (Madison 1981), morphological (Cameron and Chase 1998), and molecular (Nielsen and Siegismund 1999) studies, suggest that *Vanilla* is efficiently dispersed by animals only at local, narrow scales. This is consistent with our current understanding of endemism and restricted distribution patterns of neotropical *Vanilla* species (Soto-Arenas et al. 2003).

With this in mind, the extensive distributional ranges of our Amazonian *Vanilla* seem atypical. For example, *Vanilla bicolor* has previously only been collected in northern South America (Venezuela, Guyana, Ecuador) and the extensive populations discovered in southern Peru are highly disjunct. *Vanilla palmarum* has a similar disjunct distribution, known from Mato Grosso, French Guyana, and now southern Peru. Either these widespread species have more effective long-distance dispersal mechanisms than imagined, or their previously continuous ranges have been fragmented by vicariance events in the geological past. In the latter case, the apparent association between Amazonian *Vanilla* and hydromorphic conditions is intriguing in light of palynological (Rull 1998; Hoorn 2006) and paleogeographical (Hoorn 1993; Hoorn 1994) studies suggesting that semi-aquatic environments of lakes and *Mauritia*-dominated swamps were extensive during the deposition of the upper Pebas Formation in the early-mid Miocene. Indeed, an ancient, extensive wetland system covering over one million km², in the heart of the modern Amazon basin (Wesselingh et al. 2002) would have been a cradle of speciation for wetland-associated organisms and a means of range expansion for others (i.e., *Vanilla*). With Andean orogeny and the formation of the modern Amazon River, many wetland-associated organisms may have become progressively isolated and fragmented, pushed to the peripheries of their original distributions displaced by the highly pulsating, highly depositional environment that characterizes most Amazonian rivers. The extent to which this has influenced current species distribution, evolution, and diversity of Amazonian *Vanilla*, however, is limited to conjecture, especially without molecular evidence.

Conservation

Our studies of the flora of the wetlands of Madre de Dios has led to the documentation of nearly 600 species

of plants that are largely restricted to those ecosystems. This includes more than 50 species of orchids—up to half of the orchid species diversity currently known for Madre de Dios. The dearth of collection history of Amazonian *Vanilla* is lamentable, limiting our understanding of the evolution and diversification of the genus. We believe this state of affairs typifies our current understanding of the larger Amazonian flora, and especially of the ubiquitous, but little-studied wetlands occupied by Amazonian *Vanilla*. This deficit is especially alarming given the increasing rate of human development and habitat destruction in and around upper Amazonian wetlands. In Madre de Dios, gold mining directly within wetlands is an immediate threat to the flora, fauna, and the important ecosystem services provided by these understudied and largely unprotected wetlands. Furthermore, proposals to construct a \$4 billion dam in the Inambari River watershed (a tributary of the Madre de Dios River), the largest in Peru and the fifth largest in Latin America, would especially degrade regional wetland ecosystems (Barrow 1988; Dourojeanni 2009). Despite the high diversity and abundance within wetlands, the extensive *Vanilla* populations of the western Amazon have never been documented by the scientific community and are virtually unknown to local peoples. Its high visibility and abundance make it an interesting model for future ecological and molecular studies. Additionally, fruit fragrance of several species makes them good candidates as gene donors for the improvement of existing *Vanilla* cultivars or the adoption of alternative ones. Given the importance of *Vanilla* as a globally-traded agricultural product and the precarious status in which many populations exist worldwide, we urgently encourage protection and continued studies of *Vanilla*-rich Amazonian wetland habitats in Madre de Dios, Peru, as an important reservoir of genetic material.

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